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REVIEW ARTICLE

The Chemical Language of Plant Defense: Volatile Organic Compounds (VOCs) and Tritrophic Interactions

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ABSTRACT

To defend themselves against herbivores, plants have evolved a sophisticated chemical "language" that mostly consists of volatile organic compounds (VOCs). By serving VOCs as signals to attract predators and parasitoids that prey on herbivores, these herbivore-induced plant volatiles (HIPVs) establish a tritrophic relationship that benefits plants and their ecological partners. In addition to discouraging herbivores, HIPVs are essential for communicating with neighbouring plants, which may "evesdrop" on these signals and bolster their defences. By interacting with higher trophic levels, this complex system highlights the deep ecological linkages that plants use to deal with challenges. Molecular processes including the jasmonic acid signalling system, which synchronizes plant defences against herbivory, control the synthesis of HIPVs. In addition to their ecological significance, HIPVs have a lot of promise for sustainable agriculture as they can replace conventional synthetic pesticides. These natural volatiles may boost biodiversity and increase crop resilience through integrated pest management (IPM). This study offers a thorough understanding of how plants use their chemical defences to survive and thrive by exploring the mechanisms behind HIPV production, their ecological roles and potential agricultural uses. This review provides the basis for sustainable pest control strategies by exploring the "chemical language" of plant defence and emphasizing VOCs' critical role in supporting tritrophic interactions.

KEY WORDS : Secondary metabolites, Volatile organic compounds, Herbivore-induced plant volatiles, Tritrophic interactions, IPM

INTRODUCTION

Plants, being stationary organisms, have developed complex mechanisms to interact with their surroundings. One of these mechanisms involves the formation of secondary metabolites. Unlike primary metabolites that are necessary for basic cellular functions, these compounds play various roles in plant growth, development and defense. Among these roles, their contribution to the production of herbivore-induced plant volatiles (HIPVs) is particularly fascinating. In the process of co-evolution, plants and insects have developed a range of harmful and beneficial interactions (Schoonhoven *et al.*, 2005; Maffei *et al.*, 2007). In interactions between plants and insect herbivores, plants are always challenged by insect herbivores. Conversely, plants are not simply passive victims of these attackers (Dicke *et al.*, 2009; Das *et al.*, 2013). They have evolved numerous defense systems to protect themselves from being overeaten by herbivores (Kessler & Baldwin, 2002; Heil & Karban, 2010). These defense systems can be direct or indirect (War *et al.*, 2012). Direct plant defenses encompass various plant traits such as spines, thorns, trichomes, primary and secondary chemical metabolites, or proteinase inhibitors that influence the susceptibility to or the performance of attacking herbivores, thereby increasing plant fitness in environments with herbivores (Kessler & Baldwin, 2002). Indirect plant defenses involve plant traits or adaptations like providing shelter or alternative food sources (e.g. extrafloral nectar) (Turlings & Wackers, 2004; Kost & Heil, 2006; Choh & Takabayashi, 2010) or releasing induced plant volatiles upon herbivore infestation, which result in the recruitment and sustenance of natural enemies such as predators and parasitoids that attack the herbivores (Turlings & Tumlinson, 1992; Tatemoto & Shimoda, 2008; Gebreziher, 2018). Plants release volatile organic compounds (VOCs) in significant amounts: often up to 10% of the carbon they assimilate (Becker *et al.*, 2015). VOCs are emitted by all vascular plants continuously;

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however, under biotic and abiotic stress, emissions may increase significantly and the compositional blend of volatiles also changes (Malik *et al.*, 2016; Sarkar *et al.*, 2016; Mitra *et al.*, 2017, 2020, 2021; Das *et al.*, 2021; Koner *et al.*, 2022; Ali *et al.*, 2023; Debnath *et al.*, 2023). Herbivore feeding and oviposition result in the release of a specific blend of plant volatiles called herbivore-induced plant volatiles (HIPVs) and oviposition-induced plant volatiles (OIPVs), respectively (Fig. 1) (Dicke & Sabelis, 1988; Turlings *et al.*, 1990; Ali *et al.*, 2023). Insects feeding on plants introduce emission of new VOCs in the HIPV blends (Debnath *et al.*, 2023). Feeding by herbivores triggers plant defense responses that lead to the systemic release of various volatiles, making the plant attractive to natural enemies of the herbivores (Schoonhoven *et al.*, 2005; Heil & Bueno, 2007). Numerous arthropod natural enemies use the HIPVs to locate and feed on their prey or parasitize their hosts (Dicke & Sabelis, 1988; Turlings & Wackers, 2004; Das *et al.*, 2013; Dicke, 2015). To date, a multitude of studies have investigated the attractiveness of HIPVs to natural enemies such as predators, or parasitoids (Turlings *et al.*, 1990; Van Poecke *et al.*, 2001; Yu *et al.*, 2010).

Primary and Secondary Metabolites

Metabolites are the products and intermediates of metabolism. Plants, like all living organisms, have primary metabolism, which involves the formation and breakdown of a limited set of chemicals such as nucleic acids, proteins, carbohydrates and carboxylic acids. The majority of a plant's biomass consists of primary plant substances, which are compounds associated with essential cellular functions like growth and energy metabolism (Hussein & El-Anssary, 2018). Based on primary metabolism, plants have evolved secondary metabolic pathways that produce a wide range of secondary plant substances. These compounds are not universally found in all higher plants but restricted to certain plant taxa, or occurring in certain plant taxa at much higher concentrations than in others, and they have no apparent role in primary metabolism (Schoonhoven *et al.*, 2005; Thirumurugan *et al.*, 2018). While the vast and diverse assortment of organic compounds produced by plants do not appear to participate directly in growth and development, they often play an important role in plant defense. Secondary metabolism is not essential for short-term survival but is crucial for the long-term survivability, particularly in plant defense against predators and herbivores as well as in various biological events such as pollination and communication between host and pathogen (Schoonhoven *et al.*, 2005; Pagare *et al.*, 2015). Secondary metabolites are synthesized from primary metabolites by various pathways mainly from the shikimic acid pathway and mevalonic acid pathway. Most secondary metabolites are formed from by-products or intermediates of primary metabolism (Hartmann, 1996). The basic structures of the three major classes of secondary metabolites-terpenoids (isoprenoids), alkaloids and phenylpropanoids- are formed from the products of carbon and nitrogen metabolism. The synthesis of secondary compounds often involves interconnected pathways, forming polydimensional networks (Hartmann, 1996). A simplified classification distinguishes nitrogen-containing compounds, terpenoids and phenolic compounds.

Terpenoids: Terpenoids, also known as isoprenoids, form a highly diverse group of plant secondary metabolites that result from the repeated merging of isoprene units. These compounds serve various ecological functions such as acting as deterrents to herbivores, providing protection against microbial infections and facilitating interactions with pollinators. In response to herbivory, plants often increase the production of specific terpenoids, leading to the release of VOCs that either attract natural enemies of the herbivores or act as repellents. For example, following herbivore attacks, the levels of monoterpenes and sesquiterpenes in leaves often increase, thus enhancing indirect defense mechanisms (Böttger *et al.*, 2018; Thirumurugan *et al.*, 2018).

Alkaloids: Alkaloids, nitrogen-containing compounds, are renowned for their toxic properties and their ability to effectively deter herbivores. They typically disrupt the nervous system or metabolic processes of herbivores. The biosynthesis of alkaloids is tightly regulated and can be significantly stimulated by herbivore damage. For instance, herbivory triggers a surge in nicotine levels in tobacco plants, contributing to their defensive properties by poisoning or deterring herbivores (Sun *et al.*, 2024). Alkaloids are produced from amino acids and exhibit a wide array of bioactivities including anti-feedant and toxic effects (Croteau *et al.*, 2000).

Phenylpropanoids: Phenylpropanoids constitute a broad category of aromatic compounds derived from the shikimate pathway, encompassing substances such as lignins, tannins and flavonoids. These metabolites play crucial roles in maintaining plant structural integrity, providing UV protection and serving in defense mechanisms. Herbivore attacks can stimulate the accumulation of phenylpropanoids such as tannins, which reduce herbivore digestion efficiency by binding to proteins and inhibiting digestive enzymes (Croteau *et al.*, 2000; Böttger *et al.*, 2018). Additionally, mechanical damage triggers enhanced lignin biosynthesis, reinforcing cell walls and increasing resistance to further herbivore penetration.

Flavonoids: Flavonoids, a specific subgroup of phenylpropanoids, include compounds like anthocyanins and flavonols. These molecules not only contribute to pigmentation to attract pollinators but also possess antioxidant and defensive functions. Herbivory prompts the synthesis of particular flavonoids, which can act as feeding deterrents or disrupt herbivore physiology (Tiwari & Rana, 2015; Böttger *et al.*, 2018). Further, flavonoids can influence plant-microbe interactions, indirectly contributing to defense by modulating symbiotic relationships (Schoonhoven *et al.*, 2005).

The secondary metabolism of plants exhibits remarkable plasticity and responsiveness to various degrees including types of herbivory. Damage caused by above-ground and/or below-ground herbivores can impact the levels of primary and secondary metabolites in plants, and alterations in these chemicals can influence the interactions between above-ground and below-ground herbivores (Schoonhoven *et al.*, 2005; Huang *et al.*, 2013). When plants are attacked by herbivores, their metabolism undergoes a complex reorganization, redirecting resources from growth and reproduction to defense mechanisms. The response to herbivory involves a regulated process of activating the biosynthesis of secondary metabolites, which includes hormonal signalling pathways and reallocating resources. Following herbivore damage, plants trigger induced defenses that enhance the production of secondary metabolites. These defenses are activated through hormonal signalling, particularly the jasmonic acid (JA) pathway, which plays a crucial role in controlling the production of terpenoids, alkaloids and phenylpropanoids (Schoonhoven *et al.*, 2005; Böttger *et al.*, 2018). The responses mediated by JA result in the increased expression of genes related to defense and the accumulation of secondary metabolites that repel herbivores or attract their natural predators (Croteau *et al.*, 2000; Böttger *et al.*, 2018).

Volatile Organic Compounds (VOCs)

Numerous secondary metabolites and some intermediates of primary metabolism can be emitted by plants, possessing a vapor pressure high enough to influence other organisms as volatile substances. VOCs are small molecular-weight (50 to 200 Da) chemicals that plants emit into the air as gases. These substances are crucial for plant ecology, affecting interactions among plants, herbivores and additional organisms. VOCs are released from various plant structures such as leaves, flowers, roots and stems, and their emission may be triggered by regular growth or by environmental pressures like herbivore assaults, pathogen intrusion and abiotic factors such as dry conditions and temperature variations (Paré & Tumlinson, 1999; von Mérey *et al.*, 2013; Mitra *et al.*, 2017; Davidson-Lowe & Ali, 2021; Mitra *et al.*, 2022).

VOCs are biosynthesized as secondary metabolites from precursors that are either intermediates or byproducts (phosphoenolpyruvate, pyruvate, acetyl co-A, etc.) of its primary metabolism. There are primarily four major biosynthetic pathways that give rise to majority of VOCs: (i) Shikimate pathway producing VOCs belonging to benzoid and phenylpropanoid classes; (ii) the methylerythritol phosphate (MEP) pathway producing hemiterpenes, monoterpenes, diterpenes and volatile carotenoids; (iii) the mevalonic acid (MVA) pathway that gives rise to sesquiterpenes and (iv) lipoxygenase (LOX) pathway that ultimately leads to production of methyl

Table 1: Major biosynthetic pathways involved in production of VOCs in plants (Dudareva *et al.*, 2013).

Biosynthetic Pathway	Precursors	Intermediates	Classes of VOCs Produced	Example of VOCs
Shikimate Pathway	Phosphoenol-pyruvate	Phenylalanine → Cinnamic acid (CA) → Benzoyl-CoA	Phenylpropanoid/ Benzenoid compounds	Benzylbenzoate; Phenylalanine; Phenylethylamine; Eugenol; Methylcinnamate, etc.
Mevalonic Acid (MVA) Pathway	Acetyl-CoA	3-Hydroxy-3-Methylglutaryl-CoA (HMG CoA) → Mevalonate →→ Isopentenyl Pyrophosphate (IPP)	Volatile Sesquiterpenes (C_{15})	β-Caryophyllene; Farnesene etc.
Methylerythritol Phosphate (MEP) Pathway	Pyruvate	1-Deoxy-D-Xylulose 5-Phosphate → MEP →→ IPP → Geranyl Diphosphate → Geranylgeranyl Diphosphate	Carotenoids/ Hemi-, Mono- and Di-terpenes	Geraniol; Limonene; Isoprene; Gibberellic acid; Kaurene etc.
Lipoxygenase (LOX) Pathway	Acetyl-CoA	Malonyl CoA → Linoleic/ Linolenic Acid →→ 9- and 13-Hydroperoxy linolenic acid	Green Leaf Volatiles (GLVs)/Methyle Jasmonate (MeJa)	Hexanal; (*E*)-2-Nonenal; 3,6-Nonadienal; 3,6-Nonadienol; (*E*)-2-Hexenyl Esters; Nonedienyl Esters; Methyl Jasmonate etc.

jasmonate (MeJa) and green leaf volatiles (GLVs) (Dudareva *et al*., 2013) (Table 1).

A vital ecological role of VOCs is in plant defense. When herbivores attack plants, they emit certain VOCs that either deter the herbivores or attract their predators and parasitoids that prey on the herbivores (Pare´ & Tumlinson, 1999; Kost & Heil, 2006). For instance, when under attack, wheat seedlings release VOCs that dissuade aphids (Davidson-Lowe & Ali, 2021). Conversely, plants often produce VOCs that attract even more herbivores, along with releasing substances like linalool oxide and farnesene, which draw natural enemies that assist in managing herbivore populations (Fig. 1) (Kost & Heil, 2006; Mitra *et al*., 2017; Davidson-Lowe & Ali, 2021; Mitra *et al*., 2022). During pollination, floral VOCs serve as scent signals to attract certain pollinators but they might also unintentionally lure herbivores like aphids or beetles, presenting a dilemma for the plant (Fig. 1) (Kost & Heil, 2006; Davidson-Lowe & Ali, 2021). Some plants navigate this issue by adjusting their VOC emissions in response to environmental cues, enabling them to attract pollinators while warding off herbivores (Davidson-Lowe & Ali, 2021). VOCs also play a role in inter-plant communication, where nearby plants can "listen in" on VOC emissions and initiate their own defensive actions in advance. This system of communal awareness aids plants in better resisting herbivore attack and bolsters ecosystem resilience (Schoonhoven *et al.*, 2005).

Herbivore-Induced Plant Volatiles (HIPVs)

Herbivore-induced plant volatiles (HIPVs) represent a specific category of VOCs that plants emit in response to herbivore attacks. These volatile substances are vital for plant defense, acting indirectly by luring natural predators or parasitoids of the herbivores, which can help to alleviate herbivore damage to the plant. HIPVs are released not only from the areas affected by herbivore feeding but also from other undamaged regions of the plant as a result of systemic signalling that propagates throughout the organism (Karmakar *et al*., 2018).

HIPVs are essential in the ecological relationships between plants and insects. For instance, when the plant *Solena amplexicaulis* (Lam.) Gandhi is consumed by herbivores such as *Aulacophora foveicollis* Lucas (Coleoptera: Chrysomelidae), it starts to release particular HIPVs from its unscathed upper foliage between 24 to 120 hours after herbivore feeding. These HIPVs consist of compounds like linalool oxide, nonanal and *trans*-2-nonenal, which in some cases may attract the herbivore itself or, in other cases, its natural enemies (Karmakar *et al*., 2018). Identifying and harnessing these HIPVs can offer important opportunities for creating environment-friendly pest management solutions.

HIPVs often serve as efficient signals for luring predators or parasitoids of the herbivores. For example, certain HIPVs emitted by plants under caterpillar attack can draw parasitic wasps that oviposit inside the caterpillars, eventually leading to their demise. This tritrophic interaction is a well-researched instance of how plants utilize HIPVs to invite natural predators of herbivores (Grof-Tisza *et al*., 2024). Additionally, HIPVs can also act to repel other herbivores. In certain situations, plants emit volatiles that deter herbivores after an initial attack, informing other herbivores that the plant is no longer a suitable food option. This dual function of HIPVs– as both attractants and deterrents–renders them adaptable assets for managing interactions between plants and herbivores (Aartsma *et al*., 2017).

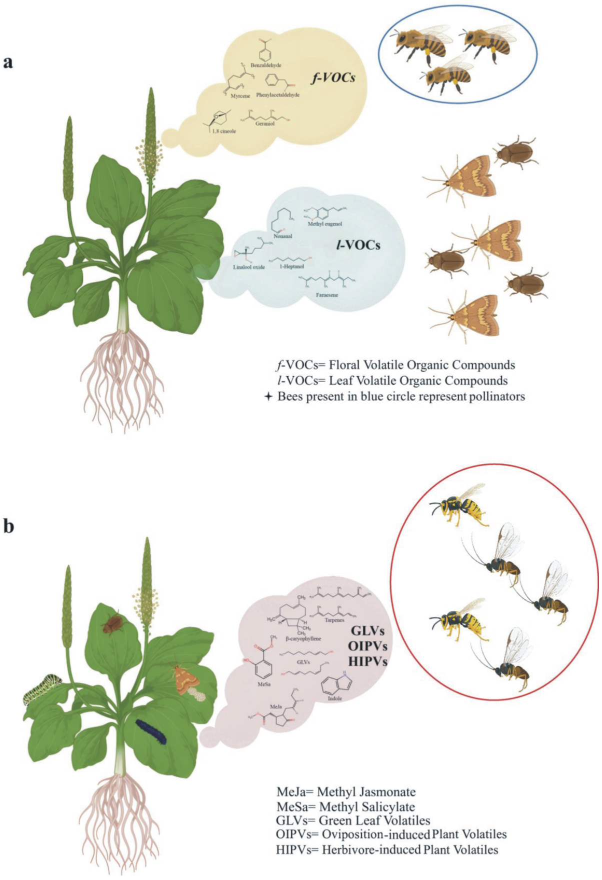

Fig.1. Plant-herbivore-predator tritrophic dynamics: a: Plants release VOCs both from leaves and flowers, while floral volatiles are important cues to pollinators (in blue circle), both kind of volatiles attract herbivores and ovipositors. b: As plants are infested with herbivores, they release herbivore-induced plant volatiles (HIPVs) in response to tissue damage or/and oviposition-induced plant volatiles (OIPVs) in response to oviposition by the insects. These specialized VOCs in turn signals predatory insects (in red circle) to invade the scenario and prey upon herbivores.

The systemic characteristic of HIPV release is another significant aspect. Studies indicate that when herbivores feed on any part of a plant, the unaffected leaves can initiate the emission of HIPVs, despite not being directly harmed. This systemic reaction enables the plant to proactively defend itself throughout its structure, improving its survival prospects against extensive herbivore assaults (Turlings & Tumlinson, 1992; Rashid & Chung, 2017; Karmakar *et al*., 2018). HIPVs also signal conspecific neighbouring plants about the potential threat and thus induce them to invest more in their defense against herbivory. HIPVs from *Mythimna separata* Walker (Lepideoptera: Noctuidae) damaged maize plants prepare the neighbouring undamaged maize plants for enhanced defence response beforehand (Ramadan *et al*., 2011).

Plant-Herbivore-Predator Tritrophic Interaction

To enhance their defenses against attacks, plants have developed a range of protective traits, including chemical defenses such as non-volatile metabolites (like toxins, digestibility inhibitors and deterrents) or HIPVs, as well as physical defense traits including trichomes, thorns or waxy coatings (Kessler & Baldwin 2002; Runyon *et al*., 2010; Wei *et al*., 2013). The relationship among plants, herbivorous insects and their predators forms a captivating tritrophic interaction crucial for understanding ecological processes. Central to these interactions are VOCs, which are chemical signals released by plants in response to herbivory. These volatiles act as direct defenses and are also vital for indirect defense strategies by attracting the natural enemies of herbivores, and thus create a complex ecological network (Schoonhoven *et al*., 2005). VOCs are essential in tritrophic interactions among plants, herbivores and their natural foes (predators or parasitoids). When insect herbivores attack plants, they emit HIPVs that signal to attract the predators and parasitoids of those herbivores. This mechanism of indirect defense aids in controlling herbivore populations while minimizing the need for plants to invest in expensive direct defenses (He *et al*., 2019; Buonomo *et al*., 2019).

Plants thrive in complex environments where they face challenges from herbivores and pathogens. Meanwhile, herbivores are hunted by various carnivorous creatures including predatory insects and parasitoids. This tritrophic system operates through sophisticated biochemical signalling pathways, with plants often using volatile emissions as a primary method to lure the natural enemies of herbivores (Agrawal, 2000; Heil, 2008). Plants constantly emit a mixture of VOCs that serve multiple ecological functions. In response to herbivory, the release of HIPVs functions like an alarm system, signalling both nearby plants and the natural enemies of herbivores (He *et al*., 2019; Buonomo *et al*., 2019). Plants have developed the capability to express distress through the release of VOCs. Compounds such as terpenes and green leaf volatiles (GLVs) are released in reaction to herbivore attacks, which subsequently attract carnivorous insects including parasitic wasps, predatory mites and beetles (Fig. 1) (Agrawal, 2000; Tiku, 2021). These substances bolster the plant's chances of survival by mitigating the herbivore burden through a strategy known as indirect defense, wherein plants utilize the predation behavior of higher trophic levels to alleviate herbivore pressure. As VOCs travel through the air, they can gradually degrade mainly by interacting with reactive gases and chemicals, which alters the chemical composition and ratio of individual compounds in the HIPV blend, thus making it more difficult for the parasitoids to track (Blande *et al*., 2014; Aartsma *et al*., 2017).

Herbivory initiates intricate metabolic transformations in plants, resulting in the formation of secondary metabolites, including VOCs such as terpenes, green leaf volatiles (GLVs) and derivatives of jasmonic acid. JA pathway serves as a key hormonal signaling mechanism that is essential for both direct and indirect plant defenses (Agrawal, 2000; Heil, 2014; Buonomo *et al*., 2019). When subjected to herbivore attacks, there is an upsurge in JA biosynthesis, which promotes the generation of volatiles that attract natural predators and parasitoids. Additional compounds including methyl salicylate (MeSA) and linalool play significant roles in attracting beneficial organisms like parasitic wasps and predatory mites, which help to manage herbivore populations (Buonomo *et al*., 2019; Tiku, 2021). JA signalling is also vital to initiate these HIPVs and coordinate the plant's defensive strategies (Buonomo *et al*., 2019). Moreover, salicylic acid (SA) and other hormonal pathways collaborate to refine these responses based on the specific type of herbivore involved (Ament *et al*., 2004; Mitra *et al*., 2020). Both JA and SA are essential for orchestrating direct and indirect defenses. JA constitutes a core element of signal-transduction pathways that govern tritrophic relationships among plants, herbivorous arthropods, and their predators following herbivore damage to the plant. In reaction to herbivore attacks, JA biosynthesis triggers the production of secondary metabolites like proteinase inhibitors and polyphenol oxidase in tomato plants (Stout *et al*., 1994; Constabel *et al*., 1995). Additionally, this hormone plays a role in systemic signalling, enabling plants to activate defenses in areas that have not yet been harmed. JA works in synergy with other plant hormones including SA and ethylene (ET), though interactions between these pathways can prioritize certain defenses based on the nature of the attacker (War *et al*., 2013). The octadecanoid and phenylpropanoid pathways, regulated by JA and SA, respectively, produce various intermediary compounds. Some of these compounds possess antibiotic properties against insect pests, while others deter oviposition (van Poecke & Dicke 2002; War *et al*., 2013). Generally, defenses mediated by JA are enhanced in response to herbivores that chew, like caterpillars, whereas SA-mediated defenses are primarily linked to reactions against pathogens and piercing-sucking insects such as aphids (Agrawal, 2000; War *et al*., 2013). This hormonal interaction introduces further complexity to the relationships among plants, insects and their predators, emphasizing the intricacy of plant defense strategies.

A well-examined instance of this interaction is maize's (*Zea mays* L.) reaction to caterpillar feeding. When it is attacked, maize emits a blend of VOCs that attract parasitic wasps, which then lay their eggs inside the herbivorous larvae, ultimately causing the larvae's demise (He *et al*., 2019). In another investigation, it was demonstrated that feeding by either *Ostrinia furnacalis* Guenée (Lepidoptera: Crambidae) or *M. separata* on maize plants led to an increased release of HIPVs such as esters, terpenes, alkanes and aldehydes, which subsequently attracted the predatory beetle *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) (Foba *et al*., 2023). Likewise, lima beans (*Phaseolus lunatus* L.) emit HIPVs that attract predatory mites to combat herbivorous spider mites (Agrawal, 2000). In wild tobacco (*Nicotiana attenuata* Torr. ex S. Watson), the production of linalool, a frequently emitted volatile, has been shown to attract predators like *Geocoris* bugs that feed on the herbivore *Manduca sexta* (L.) (Lepidoptera: Sphingidae) (He *et al*., 2019). Noge & Tamogami (2018) opined that blue shield bug, *Zicrona caerulea* L. (Hemiptera: Pentatomidae), predates upon the flea beetle, *Altica oleracea* (L.) (Coleoptera: Chrysomelidae), an herbivore infesting common evening primrose, *Oenothera biennis* L., can discriminate and locate infested plants from uninfested ones (Noge & Tamogami, 2018).

The specificity of HIPVs plays a crucial role in tritrophic interactions. Various herbivores produce unique volatile blends, and predators and parasitoids have adapted to link specific VOCs or their comparative ratio in the blend with the presence of their prey. For example, the volatiles emitted by maize in response to caterpillar feeding are more effective to attract the parasitic wasp *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae) than those generated due to aphid feeding (Heil, 2008). This specificity allows plants to effectively recruit the most suitable natural enemies, thus enhancing their defensive strategies (Gols *et al*., 2012). Plants must also navigate trade-offs in their defensive responses. In some cases, the release of volatiles may inadvertently attract herbivores or pathogens, creating a complex balancing act between drawing in beneficial and harmful organisms. The ecological trade-offs of producing HIPVs are still under investigation, with studies indicating that herbivores exert evolutionary pressure that fine-tunes these signalling mechanisms (Agrawal, 2000; Buonomo *et al.*, 2019). Moreover, many carnivorous arthropods use cues linked to their herbivore targets or their microhabitats for locating prey. The induction of carnivore-attracting compounds due to herbivore damage is significantly influenced by jasmonic acid and the octadecanoid pathway (Turlings *et al*., 1995; Takabayashi & Dicke, 1996; Dicke, 1999; Arimura *et al*., 2000; Gols *et al*., 2012). For instance, the attraction of predatory mite *Phytoseiulus persimilis* Evans (Mesostigmata: Phytoseiidae) to volatiles induced by spider mites has been observed across various plant species (Sabelis & van de Baan, 1983; van den Boom *et al*., 2002; Gols *et al*., 2003). Research has also indicated that the presence of parasitoids reduces herbivore performance, along with an increase in parasitoid attraction to HIPVs, which serve as indirect defenses (Dicke & Baldwin, 2010).

Use in Biological Pest Control

In agricultural pest management, HIPVs are being increasingly studied as part of Integrated Pest Management (IPM) strategies. Instead of relying solely on synthetic chemical pesticides, which can negatively impact ecosystems and non-target species, HIPVs can be exploited for natural control of pest populations. HIPVs facilitate the relationships among plants, herbivores and their predators. Gaining insight into how volatiles influence plant defense strategies has significant benefits for both ecological studies and agricultural practices (Dicke, 2015). In natural environments, these relations play a vital role in preserving biodiversity and controlling herbivore populations. By attracting predators, plants can manage herbivory effectively without relying on direct defense strategies, which can be metabolically expensive (Heil, 2008). For one instance, the biocontrol agent *Altica cyanea* L. (Coleoptera: Chrysomelidae), a beetle that feeds on invasive plants like *Ludwigia* species in rice fields, is attracted to HIPVs released by weeds (Mitra *et al.,* 2020). By manipulating these VOCs, the effectiveness of biological weed control methods in agricultural settings can be enhanced, consequently reducing the need for chemical interventions (Mitra *et al*., 2017). In farming contexts, utilizing tritrophic interactions presents an environment-friendly alternative to the use of chemical pesticides. Crops modified to boost HIPV production, or those treated with substances that mimic herbivore-induced volatiles, can draw in natural pest predators, thereby diminishing the reliance on insecticides (Agrawal, 2000; Tiku, 2021). A plant's reaction to herbivory, in terms of HIPV release, has been recognized as a critical factor for prey elimination by predators, prompting research aimed at enhancing crop quality through improved HIPV emission, to develop plants better suited for interactions with biological control agents. One of the seminal studies on HIPVs was conducted to explore how the predatory mite *P. persimilis* eliminates the spider mite *Tetranychus urticae* Koch (Trombidiformes: Tetranychidae) in cucumber (Dicke, 2015). Another investigation observed that the release of plant volatiles in response to infestations by cotton aphids, *Aphis gossypii* Glover (Hemiptera: Aphididae), successfully attracted the predatory six-spotted ladybird beetle, *Cheilomenes sexmaculata* (Fab.) (Coleoptera: Coccinellidae) (Yasa *et al.,* 2024). James (2003) examined the role of HIPVs such as methyl salicylate and (*Z*)-3-hexenyl acetate in attracting beneficial predatory insects for biocontrol. This research indicated that methyl salicylate attracted the big-eyed bug, *Geocoris pallens* Stal (Hemiptera: Geocoridae), as well as hoverflies, while (*Z*)-3-hexenyl acetate served as an attractant for the mirid *Deraeocoris brevis* (Uhler) (Hemiptera: Miridae) and the minute pirate bug, *Orius tristicolor* (White) (Hemiptera: Anthocoridae). Moreover, both substances seemed to be appealing to the mite-eating ladybeetle, *Stethorus punctum picipes* Casey (Coleoptera: Coccinellidae) (James, 2003).

Not only in recruiting natural enemies, HIPVs also bolster the direct defense system of the plants, which can be exploited by administering synthetic HIPVs. One of the very first case of an HIPV was effectively executed for pest management in commercial greenhouse environments, where the role of artificial mirid-induced HIPVs was examined on the direct defense system of tomato plants in green house facilities. Healthy tomato plants that were treated with 1-hexanol, (*Z*)-3-hexenol, (*Z*)-3-hexenyl acetate, (*Z*)-3-hexenyl propanoate, (*Z*)-3-hexenyl butanoate, hexyl butanoate, methyl jasmonate and methyl salicylate showed a rise in the expression of defensive genes compared to those that were not exposed (Pérez-Hedo *et al.*, 2021). In greenhouse experiments, the exposure of sweet pepper plants to the green leaf volatile, (*Z*)-3-hexenyl propanoate significantly reduced the infestation levels of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), *Frankliniella occidentalis* (Pergande) (Thysanptera: Thripidae) and *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) compared to non-exposed plants (Riahi *et al.*, 2023). In a two-year field study, *N. attenuata* plants generated twice the number of buds and flowers when native *Geocoris* spp. predators decreased herbivore populations by 50% in response to emitted HIPVs compared to HIPV-silenced plants (Schuman *et al.*, 2012). The use of synthetic JA, SA and its derivatives to boost volatile emissions in crops, thereby enhancing either direct defense or their attractiveness to beneficial insects is also in the cards. The introduction of predator-attracting plants into crop systems, known as "companion planting," is another strategy being explored to utilize these interactions for pest management. Jaworski *et al.* (2019) tested a combined system of artificially dispensed methyl salicylate as an attractant and the companion plant *Calendula officinalis* to attract more ladybird beetle ultimately enhanced aphid control in apple orchards. A recent study showed that potato plants treated with exogenous *cis*-Jasmone were more resistant to the green peach aphid, *Myzus persicae*, which showed lower settlements, lower mean relative growth rate (MRGR), lower intrinsic rate of increase (*r*) and fewer nymph production (Khurshid *et al.,* 2024). In agriculture, synthetic blends of VOCs mimicking natural plant volatiles are being explored as eco-friendly pest management solutions. For example, a mixture resembling the scent of insect-damaged *Lathyrus sativus* L. flowers has been utilized to entice *Aphis craccivora* Koch (Hemiptera: Aphididae), while substances like methyl jasmonate and farnesene are being evaluated for their potential to repel herbivores such as aphids (Mitra *et al.*, 2022).

Another aspect of information about these HIPVs and their attracting potential towards herbivores is that they can be used to formulate species-specific blends to be used in lures and baited traps in an IPM programme, which exploit aggregating properties of the insects. Adults of *A. craccivora* were attracted towards a synthetic blend of benzyl alcohol, 1,3-diethylbenzene, thymol and 1-hexadecene at a ratio of 142.49:62.03:1.18:1, which ultimately could be useful in developing ecofriendly baited traps (Mitra *et al*., 2020). In long-range wind tunnel bioassays, females of *Spilosoma obliqua* Walker (Lepidoptera: Arctiidae) were attracted towards blends of HIPVs namely (*Z*)-3-hexenal, 1-hexanol, (*Z*)-3-hexenyl acetate, 2-octanol and ocimene. This establishes the blend's potential to be used in a HIPV-seeded baited trap (Mobarak *et al*., 2022).

HIPVs are vital for mediating the complex relationships among plants, herbivores and their predators. By utilizing these volatiles, plants can lure beneficial insects that prey on herbivores, providing a sustainable substitute for traditional pest control methods. The application of synthetic HIPVs or compounds that mimic these volatiles in agriculture has the potential to lessen the dependence on chemical pesticides and improve crop resilience through direct and indirect defense mechanisms. Research demonstrates that genetically modified crops, synthetic mixtures and companion planting can leverage these ecological interactions, showing the advantages of HIPVs in enhancing pest management strategies. Ongoing investigation of HIPVs in both natural ecosystems and agricultural settings can lead to environment-friendly solutions that bolster biodiversity and increase crop yields.

CONCLUSION

HIPVs are an advanced defensive mechanism that plants have evolved in response to herbivore feeding. These volatile substances not only repel herbivores but also act as signals that attract their natural enemies such as predators and parasitoids, thus creating vital connections in the food web involving plants, herbivores and carnivores. The capacity of HIPVs to communicate within an individual plant as well as between neighbouring plants underscores their importance in ecological systems, enhancing the survival and resilience of plants. The increasing research surrounding HIPVs highlights their potential for use in agriculture specifically in integrated pest management (IPM) techniques. By harnessing these natural defense strategies, we can create environment-friendly alternatives to chemical pesticides, which can help to reduce ecological damage while safeguarding beneficial organisms. Ongoing investigations into how HIPVs are produced and their roles in ecosystems could lead to groundbreaking, sustainable farming methods that can improve crop resilience, protect biodiversity and support the long-term health of ecosystems.

DECLARATION OF INTEREST

The authors state that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing does not apply to this article as no datasets were generated or analyzed during the current study.

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